THE TAXONOMY AND DISTRIBUTION OF THE GRYLLOBLATTIDAE

(ORTHOPTERA)

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During the approximately 35 years since the Grylloblattidae were first recognized as a distinct group, the morphology of these insects has been studied in detail, and at least the more important facts of their biology and ecology have become known. Scareity of adequate samples of several named forms makes much more collecting essential to a thorough knowledge of the taxonomy and distribution of the Grylloblattidae, but those aspects are here reviewed with the hope of providing a basis, as well as a stimulus, for further investigations.

I began the present paper, which supplements my "Synopsis" of 1937, after studying the first adult female of *Galloisiana* known to be represented in American collections. This specimen was collected on Mount Fujiyama, Japan, by P. J. Darlington, of the Museum of Comparative Zoology, Harvard College, and it was loaned by Joseph Bequaert, curator of insects at that institution.

I also wish to thank the following persons who have generously loaned material or contributed notes and specimens: W. J. Brown, Science Service, Ottawa, Ontario; G. Clifford Carl, Provincial Museum, Victoria, British Columbia; J. E. Elsea, University of California; J. D. Gregson, Dominion Entomological Laboratory, Kamloops, British Columbia; Donald J. Pletsch, Montana State College, Bozeman, Mont.; and G. J. Spencer, University of British Columbia, Vancouver, British Columbia. John L. Bauer, of Tokyo, Japan, has transmitted notes on the distribution of Japanese Grylloblattidae, obtained through the kindness of Kenji Nakamura of Kyoto Imperial University. I am indebted to T. Y. Hsiao, now of Nankai University, Tientsin, China, for translating several Japanese works. My colleague, H. S. Barber, has again been helpful in connection with aspects of geographic distribution.

NOTES ON GENERIC CHARACTERS

The female of Galloisiana nipponensis in alcohol is better preserved than the dry male holotype of that species, and it affords several additions to our knowledge of generic characters. In Galloisiana the base of the middle valve of the ovipositor (fig. 2, x) is remote from the bases of the dorsal and ventral valves, unlike the condition in Grylloblatta (fig. 3). In ventral view, sternum VIII of Galloisiana has a heavily sclerotized, narrowly V-shaped, specialized area (fig. 7, y). This is in contrast to sternum VIII of Grylloblatta, which is

Fig. 1. Galloisiana nipponensis (Caudell and King), adult female. Length, to apex of posterior tergum, 22 mm. (Outlines of three apical segments of cerci sketched by the author, because of indistinct photograph.) Photograph by Marcel L. F. Foubert, U. S. Department of Agriculture. weakly obtuse mesially and has a weakly sclerotized median portion (fig. 10, z) bordered laterally by strongly sclerotized, arcuate, longitudinal bands. The lacinia of *Galloisiana* has two well-spaced preapical teeth, in contrast to one in *Grylloblatta* (figs. 6, 9). The first cervical sclerite (fig. 5, 1c) has heavy spinelike setae borne along a distinct lateral margin, instead of weak setae not confined to the margin as in *Grylloblatta* (fig. 8). The abdominal sterna of *Galloisiana* show large, sparse setae, arranged mainly in two transverse rows on each sternum. The species of *Grylloblatta* have many small ventral abdominal setae arranged with little indication of rows.

It is clear from a study of the female of Galloisiana nippo*nensis* that the cerci include only eight segments, which is true of Grulloblatta. In dry material the limits of the more basal segments are difficult to determine, and it was previously thought (Caudell & King, 1924; Gurney, 1937, p. 163, fig. 3) that nine segments occur in Galloisiana. Though the fundamental difference between the two genera with respect to pronotal shape holds, as brought out in 1937, some specimens of Grylloblatta campodeiformis do not have the lateroposterior angles so nearly right-angled as shown in my illustration (1937, fig. 7) of G. sculleni. Figure 4 of G. campodeiformis occidentalis is typical of certain specimens which have the posterior half of the lateral pronotal margins sufficiently curved ventrally to create very broadly rounded lateroposterior angles when seen in a dorsal view. The pronotum of Grulloblatta nymphs does not have well-developed latero-

Plate 6

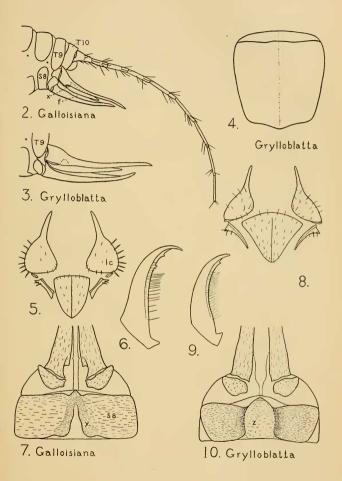
Fig. 2. Same, apex of abdomen, lateral view.

- Fig. 3. Grylloblatta campodeiformis campodeiformis Walk., adult female, same view as fig. 2, cercus omitted. Fairy Lake area, Mont.
- Fig. 4. G. camp. occidentalis Silvestri, male, pronotum, dorsal view. Mt. Baker, Wash.
- Fig. 5. Galloisiana nipponensis, female, prosternum, ventral view.
- Fig. 6. Same, male holotype, right lacinia, ventral view.
- Fig. 7. Same, female, base of ovipositor, ventral view.
- Fig. 8. Grylloblatta camp. campodeiformis, prosternum, ventral view. Same specimen as fig. 3.
- Fig. 9. Same, right lacinia, ventral view. Same specimen as fig. 3.

Fig. 10. Same, base of ovipositor, ventral view. Same specimen as fig. 3.

ABBREVIATIONS

f—membranous inner flap of lower valve. le—first laterocervical sclerite. 88—sternum VIII. T9, T10—tergum, IX, X. x—base of middle valve of ovipositor. y—sclerotized V-shaped area. z—weakly sclerotized median area. PROC. ENT. SOC. WASH., VOL. 50, NO. 4, APRIL, 1948 PLATE 6



posterior angles. The posterior margin is sinuate in *Grylloblatta*, evenly and broadly rounded in *Galloisiana*. The female of *nipponensis* agrees with male in pronotal shape.

Silvestri (1927) considered Galloisiana a synonmy of Grylloblatta and proposed Ishiana as a subgenus of the latter. I believe that Ishiana should be recognized for the present as a subgenus of Galloisiana, but study of adults will be necessary to determine the relationship to Grylloblatta and Galloisiana and whether Ishiana should be retained. As shown by the catalogue, names of the Japanese grylloblattids have been confused because of the differing opinions of writers regarding the genera.

Grylloblatta Walker

The known distribution of *Grylloblatta* is shown in figure 11. Localities from which the species have been recorded are as follows (numbers correspond to those on the map):

Grylloblatta campodeiformis campodeiformis Walker 1914

- 10. Jasper Park and Mount Edith Cavell, Alberta.
- 11. Lake Louise, Lake Agnes, and Moraine Lake, Alberta.
- Sulphur Mountain, Mount Rundle, and Banff, Alberta (Type locality: Sulphur Mountain).
- 20. Emerald Lake and the Yoho Valley, British Columbia.
- 9. Toby Creek, Selkirk Mountains, Invermere, and Paradise Mine, British Columbia.
- 8. Mount Paul, Kamloops, British Columbia.
- 7. Manning Park, Timberline Valley, British Columbia.
- 6. Grouse Mountain, near Vancouver, British Columbia.
- 5. Forbidden Plateau, Vancouver Island, British Columbia.
- 14. Fairy Lake Area, Bridger Mountains, Mont.
- 15. Spring Hill Area, Bridger Mountains, Mont.
- 16. Cascade Creek, Spanish Peaks Primitive Area, Mont.
- 17. Portal Creek, Mont.
- Eldridge, Mont. (Localities 14-18 in Gallatin National Forest, 16-18 in Gallatin Canyon).
- 19. Specimen Creek, Yellowstone National Park, Wyo.

13. East Fork Road, 10 miles east of Sula, Ravalli County, Mont. G. campodeiformis occidentalis Silvestri 1931

- 4. Mount Baker, Wash. (Type locality.)
- 21. Garibaldi Park, British Columbia.
- G. sculleni Gurney 1937

3. Scott Camp, Three Sisters, Cascade Mountains, Oreg.

- G. barberi Caudell 1924 b
 - 1. North Fork of Feather River, Plumas County, Calif.
- G. sp. (identity uncertain)
 - 2. Crater Lake, Oreg.

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Fig. 11. Map showing distribution of Grylloblatta.

With the exception of 5, 6, 16, 18, and 21, I have examined material from each area represented by a number and from most of the specified individual localities. Walker (1937) states that an adult female of *occidentalis* with somewhat longer hind legs than typical *campodeiformis* was taken in Garibaldi Park, British Columbia. Spencer (1945) says that campodeiformis has been reported from the Forbidden Plateau and Grouse Mountain, British Columbia, but no further information has become available and it is doubtful if typical campodciformis is involved, in view of the Garibaldi Park record. The Forbidden Plateau, discussed by Carl (1944), is of considerable biological interest, and if *Grulloblatta* occurs there, it may be a distinct species. The Cascade Creek and Eldridge, Mont., records were obtained from Dr. Pletsch, who carefully indicated for me on an enlarged map all of the localities near Bozeman.

The species from Crater Lake, Oreg., is that reported as campodeiformis by Elsea (1937), the material of which consisted of two females about 16 mm. long, found beneath a stone at an altitude of 6,500 feet. One specimen deposited in the National Museum has the apical half of the cerci missing. but the segments of the basal half are much shorter than in campodeiformis or sculleni. The unbroken right antenna has 29 segments, markedly less than either sculleni or barberi, both of which are large species. The condition of the specimen does not warrant description, particularly in view of the fact that adults of barberi are unknown, and more material from both Crater Lake and the Mount Lassen area is needed to clarify the situation. The type locality of *barberi* is about 20 miles southwest of Westwood. Calif., near an entrance of the Sunnyside Mine, on the North Fork of the Feather River just above the junction of Butte Creek and about 3 miles below Seneca

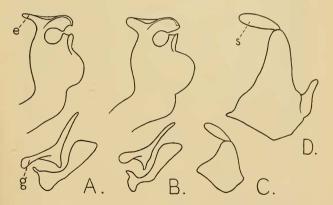
For identification of the species of *Grylloblatta*, reference is made to my 1937 key. There is still uncertainty about the correct status of *occidentalis*. Although several specimens of *camp. campodeiformis* with 30 antennal segments have been examined from Montana and from Kamloops, British Columbia, in addition to those I reported in 1937, material thus far studied suggests the subspecific distinctness of *camp. occidentalis*. Further material may show that the possession of 32-36 antennal segments is not a sufficiently constant character to distinguish *occidentalis*.

The only adult males of *Grylloblatta* of which I have studied the genitalia are two Montana specimens of *camp. campodeiformis* and one Mount Baker, Wash., specimen of *occidentalis*. The two forms apparently agree in the shape of the coxites,

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supra-anal plate, and both left and right ventral processes of the latter. Minor differences occur in the phallic sclerites of males examined. In *camp. campodeiformis* the apical lip of the copulatory process (text-fig. A, e) is more acute and the apical lobe (g) of the accessory sclerite of the right phallomere is differently shaped than those of *occidentalis* (text-fig. B). These organs and associated structures of *camp. campodeiformis* have been illustrated by Walker (1919, pl. 8; 1943, fig. 11) and by Snodgrass (1937, fig. 6). The differences would seem to be of no more than subspecific value, and a series of males of each form is needed to test the taxonomic worth of these genital features. In fact, when extensive collections of *Grylloblatta* are ultimately available from localities throughout its range, conceptions of what constitute species in this group may undergo considerable modification.

It is important to distinguish between adults and large male nymphs of Grylloblatta. In the case of camp. campodeiformis the shape of the right coxite (text-figs. C, D) is useful, in addition to the absence in the nymph of phallomeres and phallic sclerites.



Text-figures. A. Phallie sclerites of Grylloblatta camp. campodeiformis Walk., male, dorsoposterior view. B. Same view, G. camp. occidentalis Silv. C. Right coxite of nymphal male of G. camp. campodeiformis, lateral view, specimen from Fairy Lake area, Mont. D. Same view of adult male of G. camp. campodeiformis from Gallatin Canyon, Mont. e-apical lip of copulatory process. g-apical lobe of accessory selerite of right phallomere. s-stylus. It is of interest that *Grylloblatta* was collected some years before its original description. I have seen a nymphal male in the Canadian National Collection taken at Banff, Alberta, November 5, 1906, by N. B. Sanborn. Tillyard (1921) noted that Mr. Sanborn, then Curator of the Rocky Mountain Museum at Banff, made collections considerably earlier than those on which the description was based, and several specimens found by him in 1910, 1908, and 1906 are cited by Walker (1919).

Seasonal distribution and habitat of Grylloblatta: Most of the observations dealing with the seasonal distribution, ecology, and biology of Grulloblatta concern typical campodeiformis, though the other forms are evidently very similar. The most complete summary of these aspects has been given by Walker (1937), from whose paper I have drawn freely. Most specimens have been collected during the late fall or winter months: this is especially true in habitats usually dry and hot in summer, as exemplified by the collecting site at Kamloops, British Columbia, described by Gregson (1939), and at Gallatin Canyon, Mont. Of the more than 100 specimens collected by Montana entomologists, only two were taken earlier than autumn, these being found in May. The explanation of the seasonal occurrence apparently lies in the temperature and humidity requirements of these insects. Most of the habitats are of a nature that permits Grulloblatta to withdraw deeply to a region of very low temperature and high humidity. or advance to the open air, depending upon outside climatic conditions. Frequent habitats are hillsides marked by coarse rock slides with innumerable deep crevices into which the insects may penetrate for long distances during unfavorable seasons. In the Canadian Rockies the margins of glacial bogs have often yielded Grylloblatta from beneath stones or in or beneath decaving, moss-covered logs or stumps. The optimum temperature is a little above freezing, though 16° C, is tolerated if the temperature is raised gradually. Temperatures a few degrees below freezing are not injurious, though -10° C. is said to be fatal if experienced quickly. Suitable habitats evidently must combine the above temperature range with high atmospheric humidity, at least in the sheltered retreats.

Entomologists searching for *Grylloblatta* will be more likely to be successful, and will avoid much extremely hard work, if field conditions favor the likelihood of the insects being near the surface of the ground and not beneath a great deal of snow or ice. Beamer (1933), Carl and Hardy (1945), Mills and Pepper (1937), and Silvestri (1931) give photographs of the terrain where Grylloblatta occurs.¹

The midwinter activity of *Grylloblatta* is evidenced by collections made in January by J. D. Gregson at Kamloops, British Columbia, and by H. S. Barber in California. Walker (1937) states that on mild days of winter or spring, specimens sometimes are found crawling on the snow. W. L. Jellison took a male nymph 14.5 mm. long in this way in Ravalli County, Mont., January 26, 1947.

Grylloblatta has usually been collected at altitudes above 5,000 ft., but records at 1,500 ft. at Kamloops, British Cohumbia, and at less than 2,000 ft. in Plumas County, Calif., indicate that high altitudes are not essential if required ecological conditions are otherwise supplied.

An understanding of these insects, primitive vet closely adapted to their environment and appropriately called living fossils by Dr. Walker, is further clarified by information on the slow rate of growth apparently suited to a habitat where life is often at low ebb many months of the year. He reports that at least five years seem necessary for nymphs to become adult, with no eggs being laid until a year later, and an additional year being thought necessary for incubation of the eggs. The last stage nymph is described as being white except for the eyes; it lives about six weeks, probably always in the darkness of its shelter. In the laboratory one feeding in three or four months has been found most satisfactory. Under natural conditions soft-bodied insects are probably the principal food -sometimes immature insect material, and at other times various insects disabled by the cold after temporary periods of activity in boreal surroundings. Small pieces of plant material are occasionally eaten. Frequently, but by no means always, Grulloblatta is nocturnal.

Galloisiana Caudell Galloisiana nipponensis (Caudell & King) (Figures 1, 2, 5-7)

Descriptive notes (female).—General structure and appearance as in male. Right antenna with 43 segments, left with 35 (broken?); segments of apical half about three times as long as broad. (Left tarsus 4-segmented, reduced in size and lacking large lateral pulvilli, apparently the result of an injury.) Apex of abdomen (fig. 2) with 8-segmented cerci, the apical segment slightly shorter than segments 4-7. Dorsal valve of ovipositor reaching to middle of third cercal segment, apex acute middle valve attached basally to dorsal valve at about one-eight the

¹Photographs of several localities where *Grylloblatta* occurs in the Canadian Rocky Mountains appear in "On the Ridgepole of the Rockies," by W. M. Edwards, 1947 (Natl. Geog. Mag., vol. 91, pp. 745-780).

distance from the latter's base; ventral valve with mesal membranous flap (fig. 2, f) normally concealed; apical sternum (fig. 7) with narrow, median, subacute process, the apex being the point of a V-shaped area more heavily sclerotized than laterad of it, the mesal enclosed area membranous.

Coloration: Head Vandyke brown; nota and ovipositor somewhat paler. Palpi, antennae, legs, cerci, terga, and sterna pale amber; intersegmental areas of abdomen ash gray; spines and principal setae brown.

Measurements (in millimeters: Body, 22; antenna, 13; eye, 0.2 (left), 0.5 (right); pronotum, 4; hind femur, 4.5; hind tibia. 4.8; dorsal valve of ovipositor, 3.8; eercus, 10.6. Widths: Head, 4.2; pronotum, 3.6; hind femur, 1.2.

Previously unreported material examined: Mount Fujiyama, Japan, wooded southern slope, October 23-24, 1945, P. J. Darlington (1 9) (M.C.Z.).

Dr. Darlington has kindly furnished the following note :

"The grylloblattid was collected in heavy maple forests on the southern slope of Fujiyama at four or five thousand feet elevation. It was under a stone, fairly deeply set in the ground. It was the only one I saw. During the two days which I spent on Fuji, I worked up through the deciduous forest from 3,000 feet to above tree line, which as I remember it is at about 6,000. The mountain forest at four or five thousand feet is magnificent, dominated by huge maple trees and some other hardwoods. Collecting there was very good. Above tree line there was only an open einder slope, completely dry and more or less without insect life. I did not see any insects at all and I doubt if many of them exist in the loose einders.''

In addition to the Fujiyama specimen, I have seen only the type series from an altitude of about 4.500 ft. on the slope of Nantai San, a mountain located at Chuzenji, about 12 miles west of Nikko, which in turn is about 120 miles northeast of Mount Fujiyama. Kishida (1929) has recorded the species from Saitama Prefecture immediately north of Tokyo, and from the vicinity of Kyoto. Matsumura (1931) adds Takayoyama, on Honshu, and I suspect this is in the Tokyo area, though there are several Japanese mountains of that name.

Dr. Nakamura of Kyoto states that grylloblattids have been taken at the following localities (which records apparently apply to *nipponensis*): Chichibu, about 55 miles northeast of Mount Fujiyama; Japanese Alps, region about 100 miles west of Tokyo; Kisenyama, near Kyoto; Mino, near Osaka.

I do not know of any records of *Galloisiana notabilis* (Silvestri) from other than the Nagasaki area of Kyushu. The type locality is the village of Michino-o.

The habitat and habits of the two² Japanese species of Grylloblattidae are essentially like those of the Nearetic forms,

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except that the climate is milder³ and, according to Silvestri (1931), the species are more rapid in their movements than *Grylloblatta campodeiformis*. Dr. Nakamura reports that, by searching under rocks, a collector may easily find two dozen specimens a day in the Japanese Alps, and that near Kyoto, Osaka, and Nagasaki they occur on quite low mountains. He found that they readily ate live termites in his laboratory. At Chuzenji, J. L. King collected *nipponensis* within and beneath decaying logs. There are no records from the northern and decidedly boreal island of Hokkaido, and, if the group is there, a distinct endemic species may be involved.

CATALOGUE OF THE GRYLLOBLATTIDAE⁴

GRYLLOBLATTA Walker

Grylloblatta Walker, 1914 (pp. 93-99); Brues and Melander, 1915, 1932; Caudell and King, 1924; Crampton, 1915; Essig, 1942; Gurney, 1937; Silvestri, 1927. (Genotype, Grylloblatta campodeiformis Walker, monobasic.)

Grylloblatta campodeiformis campodeiformis Walker

Grylloblatta campodeiformis Walker, 1914 (pp. 93-59), 1919, 1937;
Buckell, 1922, 1925, 1928, 1930; Carl and Hardy, 1945; Caudell, 1923a, 1923b;
Caudell and King, 1924; Crampton, 1915, 1926, 1927, 1933;
Criddle, 1926; Elsea, 1937; Essig, 1926, 1942; Eyer, 1924; Ford, 1923, 1926, 1937; Gibson, 1915; Gregson, 1938, 1939; Gurney, 1936, 1937;

²In a personal letter to me, Dr. Nakamura has mentioned a third Japanese species. Since I have found no description of this form, it may be only a manuscript species. I am much indebted to Dr. Pletsch, who is currently in Tokyo, and to Mr. Niimura, a Japanese entomologist who collected the insect in Nagano Prefecture, for the considerable effort with which they are attempting to clarify the status of this supposed additional species.

³In October 1945 I spent a day in the mountains between Sendai and Yamagata, about 175 miles north of Tokyo, and was impressed by the temperate character of the vegetation. At an altitude of 3,000 ft., oaks, birches, maples, hemlocks, and other trees belonging to genera well known in North America were common, and the climate seemed comparable to that of central New England. There was little opportunity to search for grylloblattids, and none were found, though they probably inhabit that area.

⁴Page references to all but original descriptions are omitted for the sake of brevity. Except in the case of short papers, however, they are given by annotations in the bibliography. Most entomological textbooks have been omitted; also most of the many morphological papers by Crampton and Walker. The more important of Crampton's papers dealing with grylloblattids are cited by Gurney (1936), while nearly all of Walker's more important morphological papers appeared in the Annals of the Entomological Society of America. Many papers on insect morphology by other authors contain brief comments on grylloblattids, and it does not seem practical or important for the present purpose to refer to them all. Hebard, 1930; Imms, 1927a; Kennedy, 1928; Lameere, 1935; Lefroy, 1923; Mills and Pepper, 1937; Silvestri, 1927, 1931, 1934; Snodgrass, 1937; Spencer, 1945; Strand, 1937; Tillyard, 1921.

Grylloblatta campodeiformis occidentalis Silvestri

- Grylloblatta campodeiformis var. occidentalis Silvestri, 1931 (p. 293); Beamer, 1933; Essig, 1942; Walker, 1937.
- Grylloblatta campodeiformis occidentalis Silvestri, Silvestri, 1934; Gurney, 1937.

Grylloblatta sculleni Gurney

Grulloblatta sculleni Gurney, 1937 (pp. 164-166).

Grylloblatta barberi Caudell

Grylloblatta barberi Caudell, 1924b (pp. 369-371); Chopard, 1938; Crampton, 1926, 1927; Essig, 1942; Gurney, 1937; Silvestri, 1931; Walker, 1937.

Grylloblatta campodeiformis Walker, Caudell, 1923a, 1923b.

GALLOISIANA Caudell Subgenus GALLOISIANA Caudell

Galloisiana Caudell, 1924a (p. 92); Crampton, 1927; Imms, 1927b; Gurney, 1937; Silvestri, 1927. (Subgenotype, Galloisia nipponensis Caudell and King, monobasic.)

Galloisia Caudell and King, 1924 (pp. 53-60). (Preoccupied.)

Galloisiana (Galloisiana) nipponensis (Caudell and King)

Galloisia nipponensis Caudell and King, 1924 (pp. 54-59).

Galloisiana nipponensis (Caudell and King), Caudell, 1924b; Crampton, 1926, 1927; Gurney, 1937; Kishida, 1929; Matsumura, 1931.

Grylloblatta nipponensis (Caudell and King), Lameere, 1935; Silvestri, 1927, 1934; Walker, 1937.

Grylloblatta (Galloisiana) nipponensis (Caudell and King), Silvestri, 1931; Essig, 1942.

Galloisidea (Sic!) nipponensis Caudell and King, Shiraki, 1932.

Subgenus ISHIANA Silvestri

Ishiana Silvestri, 1927 (p. 113); Gurney, 1937; Walker, 1937.

Subgenotype, Grylloblatta (Ishiana) notabilis Silvestri, monobasic.

Galloisiana (Ishiana) notabilis (Silvestri)

Grylloblatta (Ishiana) notabilis Silvestri, 1927 (pp. 113-118), 1931, 1934; Essig, 1942; Walker, 1937.

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